Induced and occasional parasitism

D. T. MacDougal

(with plates 22–25)

The results of some experiments in which regenerated cuttings of several succulent seed plants were made to become xenoparasites on various hosts have been published by the author during the last two years.*

Regenerated cuttings of vines and of cacti were inserted in cavities prepared for them in the bodies of other plants used as hosts, being held in place by plaster of Paris seals, and the course of growth followed for extended periods. A consideration of the morphological and chemical features of the parasite and host of all such nutritive couples was then made, to ascertain what factors made it possible for one plant to become dependent or parasitic on another. It was notable that outside of the single anatomical feature of the possession of a water balance or accumulated supply of fluid, no morphological characters might be taken as indispensable in possible parasitism. It might be seen, however, without recourse to experimental results, that certain habits of growth, of rapid formation of wound tissue and of excretions might well prevent a plant from being fastened upon by a parasite. The chemical examinations showed that when one form was induced to become parasitic upon another, the host in every case had a sap with a lower osmotic activity than that of the xenoparasite. At the same time a cutting of a species with high osmotic pressure might fail to establish itself on another plant of lower activity. This was especially true of the sahuaro, or great tree cactus (*Carnegiea*). Its succulent stems, with soft subepidermal structures, offered most inviting conditions to the experimentalist, but the acrid secretions poured into wounded cavities generally prevented inserted cuttings from withdrawing solutions that might serve as

* See The condition of parasitism in plants. Carnegie Inst. of Washington. Pub. No. 129. 1910; The making of parasites. Plant World **13**: 207. 1910; and An attempted analysis of parasitism. Bot. Gaz. **52**: ——. 1911. (In press.)

nutriment. The sole survivors on this plant as host are two opuntias, one a cylindrical and the other a flattened form, while the failures may be numbered by the score.

Opuntias with mucilaginous juices also offered unfavorable conditions for parasites. While this work was being done, estimates of the acidity of the sap of various cacti were made of specimens taken at random without regard to the time of day, exposure to light, or temperature. No connection could be established between acidity and parasitism with such data at hand. Recently, however, Prof. H. M. Richards has carried out some work on respiration at the Desert Laboratory, in which it was found that the acidity of a cactus is four times as great at sunrise as late in the afternoon, and that the amount of acid present is affected in an important manner by the rise and fall of the temperature. These variations together with the effect of the changing acidity upon the absorptive capacity of the mucilages and of other colloids, such as those of the cell walls, might account for the entire lot of experimental cases presented. Indeed, it is not too much to say that when all of these factors are properly integrated, the possibility of dependent parasitism between two species might be predicted with fair certainty.

After the completion of the last article dealing with this subject a few of the experimental parasites still remained active. The description of the further history of these arrangements and of some unusual conditions of this kind found among native plants constitute the purpose of the present paper.

A case of parasitism of *Opuntia Blakeana* on *Carnegiea gigantea* was discovered in Roble's pass, 7 miles southwest of the Desert Laboratory, on March 19, 1911, and a visit was made to it a few days later in company with Prof. H. M. Richards for the purpose of making a detailed examination and photographs.

The sahuaro was a tall specimen with four branches, being about two hundred years old. The largest branch was about 12 feet long and arose from the trunk about 7 feet from the ground. Germination of an *Opuntia* seed had evidently taken place in the axil, and the roots had penetrated the corky layers in the angle. The growth of the opuntia had resulted in the development of two main stems, one consisting of two and the other of three joints,

which showed some atrophy. The season of 1910 had been very dry and a small cylindrical branch had arisen from the basal cylindrical part of the stem, the terminal section of which had died back. (See PLATE 22.)

The large branch, which was over a foot in diameter at its base, was cut away and the roots of the opuntia dissected out, a task of some difficulty. Some of the rootlets reached a distance of a foot from the base of the opuntia, and while many of the branches partly encircled the base of the branch of the sahuaro, yet one main root and its branches had penetrated directly inward into the tissues of the greater cactus to a depth of over six inches, being completely submerged and cut off from the air. The advance of the root had been followed by the death of the cortical cells of the host and by the formation of scar tissue enclosing the parasitic roots, and then secondary root formation had followed, which resulted in a dense mesh of fibrils, none of which were in actual contact with living tissue. (See PLATE 23.)

The contact thus made with the *Carnegiea* was undoubtedly the source from which the chief supply of solutions was obtained. The remainder of the root systems was in such position that the moisture collected in the sinus of the branch and the stem might be absorbed, but as the amount of this liquid would be small and would be available for only a few hours during the entire year, it is all but a negligible quantity in the nutrition of the opuntia. A transverse section of a portion of the cortex enclosing a penetrating root would show this organ surrounded by a flattened tube of corky tissue derived from the cortex of the host. The folds of this tube extended for several millimeters from the root.

The parasitic opuntia was brought away intact and set in the soil in the terrace of the Desert Laboratory to allow observation of its further development, and under autophytic conditions. Similar experience with a plant taken from a *Parkinsonia* showed an abrupt alteration in the amount, rate of growth, and form of the flattened stems. [Bot. Gaz. **52**: —. 1911. (In press.)] So great was the difference that the identity of the species was mistaken previous to its cultivation in the ground under the customary conditions.

An *Opuntia discata* growing from the trunk of *Acacia* was reported by Dr. W. A. Cannon in 1909 and a special excursion was

made to examine the arrangement in April 1911. The original photograph, from which a drawing has been made, showed a heavy basal stem of the opuntia issuing from a knot hole in the trunk of the tree and bearing two branches, one consisting of one joint and the other of three. (Plate 24.) The size of the stem of the opuntia would indicate that it was perhaps fifteen or twenty years old, but the limited supply of food material to be obtained from the host had operated to the loss of other flat joints that may have been formed from time to time. The more recent observation showed a main horizontal stem of four joints, from which were arising a number of new joints. A basal branch of three joints was dead and was all but detached from the plant. A single upright joint bore a small young joint rapidly enlarging. Another upright joint and the two terminal joints of the horizontal stem were in a dying condition. It seems probable that the plant yearly gives rise to more branches than may be maintained by the supply of solution derived from the host and that the arid after-summer of 1911 will be the occasion for the death of some of the joints that are being formed in the growing season of the earlier part of the year. (Plate 25.)

It was not deemed advisable to dissect this arrangement until further observations had been made, but it is probable that the development of the roots of the opuntia follow the formation of a cavity in the trunk of the acacia by the decay of the wood, and that the roots of the intruding cactus operate to cause or hasten this integration. A similar case of *Opuntia* on *Parkinsonia* has been previously described. (See Publication 129, Carnegie Inst. Washington, 1910.)

A plant of *Opuntia Blakeana* set in the side of a trunk of *Carnegiea* early in 1909 has continued a fairly even existence although no growth in the way of formation of new joints has been seen. The plant consisted of a basal cylindrical section and a terminal oval joint. The plaster, which was used to hold the xenoparasite in place when first arranged, has gradually crumbled away, but the parasite is held firmly in place by its own roots. As has been previously noted, some thickening of the basal portion of the stem is noticeable. The amount of growth to be expected from parasites is always less than that of autophytic individuals.

That some actual parasitism or derivation of nutriment takes place, is evident from the fact that similar small plants separated from the soil and exposed to the same climate desiccate within a single season, while this preparation has survived three hot summers. A small individual of *O. versicolor* set in the trunk of a *Carnegiea* in the spring of 1909 is also robust and thriving, having undergone considerable thickening of the stem, one branch, and the exposed portion of the roots. Both of the above preparations give every appearance of being permanent during the ordinary life cycle of the individuals.

Some of the most important experimental results were obtained by using regenerated cuttings of a grape (*Cissus laciniata*), from the region of Tehuacán, Mexico, as a parasite, and some new arrangements were set up early in 1911. This plant undergoes secondary thickenings of the stems in such manner that portions near the ground, or partially imbedded in it, attain a diameter of several inches, and contain large balances of water and food material. Oftentimes the thickening will take place in portions of the climbing stem many feet from the ground. The thinner portions of the stem die upon the cessation of active growth, with the consequence that sections of thickened stem may be supported by the dead tendrils high above the substratum. In some instances such thickened sections will be held by a second vine, clasped by the tendrils. The beginning of activity in these suspended stems usually consists in the formation of long adventitious roots which hang down and are capable of making a length of one or two yards. If the ground is reached, new supplies ascend through the aerial roots and the plant survives. Many of the thickened sections are held at such elevation that the supply of water and material does not suffice for the construction of roots of a length that may reach the ground, and consequently the isolated members perish. Similar behavior was exhibited by plants in the glass house at the Desert Laboratory. It is evident that such suspended sections offer some chance of contact or penetration of other living plants, thus setting up parasitism, and the previous experiments showed that this grape might be made parasitic on *Opuntia*, *Echinocactus*, and sometimes on *Carnegiea*.

A number of new preparations were made in April, 1911, in

which cuttings were inserted in resting potato tubers and also in joints of *Opuntia Blakeana*. Late in May it was found that nearly all of the cuttings in potatoes were forming short basal roots with still shorter clubshaped branches, and the cavities about them were being enlarged rapidly by decay. A few cuttings were sending out aerial roots from the upper ends. These were all transferred to joints of *Opuntia*, some in the glass houses and some in the open, late in May, 1911. All in the glass house were alive, and about half of those in the open, in August, 1911. The amount of leaf development was small and the growth of the shoots offered no features not previously described.

It is notable that in these, as well as in all previous experiments dealing with this subject, very little evidence of forcible penetration of the tissues of the host was seen. Whether by the previous action of bacteria or by excretions from the xenoparasite, the invading roots never actually bored through masses of living cells. In all cases the layer of tissue, one or more cells in thickness, nearest the roots was found to be dead and more or less disintegrated. Peirce, in his earlier work on this subject, cites instances in which roots of *Brassica* and *Sinapis* actually penetrated among living cells by a comparatively rapid growth. (Das Eindringen von Wurzeln in lebendige Gewebe. Bot. Zeit. 52^1: 169. 1894.)

It is notable that the experiments included in this research, which has been carried on for four years, were made under extremely arid conditions, in which the transpiratory loss was high. The plants that were induced to live as parasites were therefore under the double burden of securing nutriment from a host, which furnished a substratum offering physical conditions widely different from those which their absorbing organs ordinarily encounter, and of maintaining their own turgidity as a necessary condition of growth and other constructive processes. As has been amply demonstrated, the change from an autophytic to a parasitic condition is one that may be readily made by many species. The distributional movements of plants, which are constantly bringing new pairs into contact, would operate to bring eligible parasites and possible hosts together and cases of newly originated dependent nutrition may be expected from time to time.

The instances reported in this and previous papers are of this character. The instances cited were found by the examination of a small number of species. A comprehensive survey of the root habits of any region would doubtless reveal a large number of parasitic arrangements of various kinds as yet unknown to us. The recent discovery of the parasitism of *Krameria* by Dr. Cannon was made by the use of such methods, and has added a tenth to the list of families with parasitic members.

DESERT BOTANICAL LABORATORY,
TUCSON, ARIZ.

Explanation of plates 22-25

Plate 22. *Opuntia* in the angle of branch and stem of sahuaro. Drawn from a photograph.

Plate 23. Detail of roots of *Opuntia* parasitic on sahuaro. (See plate 22.) Drawn from a photograph.

Plate 24. *Opuntia* on *Acacia*. Drawn from a photograph made in 1909 by Dr. W. A. Cannon.

Plate 25. *Opuntia* on *Acacia* in 1911. Photograph by the author.

MACDOUGAL, OPUNTIA ON SAHUARO

MACDOUGAL, OPUNTIA ON SAHUARO

MACDOUGAL, OPUNTIA ON ACACIA

MacDOUGAL, OPUNTIA ON ACACIA